

Impacts of non-native fishes under a seasonal temperature gradient are forecasted using functional responses and abundances

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Abstract

Developing predictive methods to forecast the impacts of existing and emerging invasive species is of critical importance to biodiversity conservation. However, invader impacts are context-dependent, making reliable and robust predictions challenging. In particular, it is unclear how temporal variabilities in relation to temperature regime shifts influence invader ecological impacts. In the present study, we quantify the functional responses of three coexisting freshwater fishes: the native freshwater River Goby *Glossogobius callidus*, and the non-native Mozambique Tilapia *Oreochromis mossambicus* and Western Mosquitofish *Gambusia affinis*, under two temperature treatments using chironomid larvae as prey. This was used along with fish abundance data to determine temporal differences in ecological impacts of each fish species between seasons (i.e. at two corresponding temperatures). All three fish species exhibited potentially population-destabilizing Type II functional responses. Their maximum feeding rates were consistently higher in the warm temperature treatment, whereas attack rates tended to be reduced. Non-native Mozambique Tilapia had the highest maximum feeding rate under both temperature treatments

(18 °C and 25 °C), followed by the non-native Western Mosquitofish and lastly the native River Goby, suggesting greater *per capita* impacts on native prey by non-native fishes. The predatory fish abundances differed significantly according to season, with native River Goby and non-native Mozambique Tilapia generally more abundant than non-native Western Mosquitofish. By multiplying functional response maximum feeding rates with abundances of each fish species across the seasonal gradient, the relative impact potential of non-native Mozambique Tilapia was consistently higher compared to that of native gobies. Western Mosquitofish impacts were less apparent, owing to their low abundances. We demonstrate how seasonal temperature fluctuations affect the relative impact capacities of introduced species and the utility of consumer functional response and the relative impact potential metric in impact forecasting.

Keywords

Context-dependence, impact assessment, introduced species, relative impact potential, seasonal abundance, thermal regime

Introduction

Biological invasions are a central driver of global biodiversity loss (Sala et al. 2000; Turak et al. 2016; Bertelsmeier and Keller 2018; Shuai et al. 2018). This loss has not only socio-economic impacts, but also threatens ecosystem functions and services (Ricciardi et al. 2017). Biological invasions can occur through numerous pathways, such as human-mediated introduction, climate change and connectivity of systems, thus allowing extra-limital movement of species (Latombe et al. 2017). Upon arrival in a new environment, non-native species can cause ecological impact on native species assemblages through a range of biotic interactions (e.g. predation, competition and parasitism) (Vitousek et al. 1996; Thomsen et al. 2011; Havel et al. 2015; Seebens et al. 2018). Competition and predation play particularly important roles in the structuring of ecological communities (Paine 1980; Gurevitch et al. 1992). Although the impact of invaders through predation and competition is well documented, the context-dependency of these processes is often overlooked. In particular, direct biotic interactions (i.e. predation) can drive trophic cascades through alterations of prey abundance and native predator fitness (Gallardo et al. 2016; Penk et al. 2017).

Despite the considerable work conducted on invasive species, predicting ecological impacts of biological invasions has remained elusive (Simberloff et al. 2013; Dick et al. 2014). Ricciardi et al. (2013) highlighted context-dependency as the largest confound for impact predictions in invasion biology. Therefore, robust predictive methods that include environmental contexts as factors are needed in invasion studies to improve impact forecasting. In particular, temperature regime is a key abiotic context that is pervasive across all ecosystem types, and particularly in aquatic ecosystems (Lang et al. 2017). Specifically, temperature is a central determinant of the strength of predator-prey interactions and mediates food web stability (Rall et al. 2010, 2012; Englund et al. 2011). Fish have physiological mechanisms (i.e. metabolism and reproductive success) that are directly and/or indirectly dependent on temperature (Roessig et al. 2004). These mechanisms may differ between native and non-native species given differences in geographical origins and their physiological tolerances (Sorte et al. 2013). If high temperatures are more physiologically optimal for invaders, ecological impacts

may be intensified (Iacarella et al. 2015), and seasonal changes, coupled with ongoing climatic warming, are key drivers of such temperature change in aquatic ecosystems. Indeed, interaction strengths are known to vary even with slight changes to seasonal temperatures (Sanford 1999, 2002). Therefore, failure to incorporate these factors in predictive approaches limits our ability to forecast invasive species impacts under changing environmental conditions across different spatiotemporal scales (Dick et al. 2013, 2014, 2017).

Methodological developments, which incorporate native/non-native species resource utilization across context-dependencies, have recently provided robust predictive tools for invasion science (Laverty et al. 2015; Dick et al. 2017; Dickey et al. 2018; Cuthbert et al. 2019). In particular, the functional response quantifies resource consumption as a function of resource density, and, in a predator-prey context, can quantify *per capita* ecological impacts of predators towards lower trophic groups (Holling 1959; Adams 1980; Dick et al. 2013, 2014, 2017; Alexander et al. 2014; Cuthbert et al. 2018). The types and magnitude of FRs quantify whether consumers will likely stabilize or destabilize resource populations (Murdoch and Oaten 1975; Rip and McCann 2011; Uszko et al. 2017). The relationships between consumer resource uptake and resource densities results in three broad functional response 'Types', and each Type has a different effect to resource population stability: an increasing linear relationship with no handling time constraint (Type I, mechanistically exclusive to filter feeders; Jeschke et al. 2004); an inversely density-dependent response characterized by high resource consumption at low resource density (Type II, resulting in rapid resource depletion at low densities); and a sigmoidal positively density dependent relationship (Type III, where resources have a low-density refuge) (Holling 1959). Despite the two functional response components, i.e. attack rate and handling time, being strongly associated with variations in temperature (Englund et al. 2011; Rall et al. 2012; Sentis et al. 2012; South et al. 2017; Cuthbert et al. 2018), there is, however, very limited information available on how temperature mediates species interactions at the population-level (Viherluoto and Viitasalo 2001; Fussmann et al. 2014; O'Gorman et al. 2017). Temperature and/or season effects may differ depending on how species functional traits directly influence responses, and these traits may too change along environmental gradients (Chapin et al. 2000).

Classically, the functional response has been combined with the 'numerical response' to determine the 'total response' of consumers (Solomon 1949; Holling 1959). The numerical response describes the consumer population-level response to changes in resource densities, while 'total response' can be defined as the multiplication of species' numerical response with functional response (Solomon 1949; Holling 1959). Given that the numerical response, in comparison to the functional response, is difficult to ascertain, consumer abundance has recently been proposed as a proxy for numerical response in the development of the 'impact potential' and 'relative impact potential' metrics (Dick et al. 2017; Dickey et al. 2018). The 'impact potential' is the product of functional responses and abundance of consumers, while the relative impact potential compares the impact of the invader to that of a native (Dick et al. 2017). The strength of the relative impact potential metric lies in its ability to incorporate

both species abundance and functional response under different environmental conditions (e.g. temperature change) and thus predict the influence of context-dependencies on invader impact (Lavery et al. 2017). This metric provides a novel approach for assessing existing and potential ecologically damaging species through the use of actual field abundance data under different environmental conditions.

The current study focuses on one native and two non-native fish species that co-occur in irrigation ponds within the Sundays River Valley, Eastern Cape, South Africa. These are the native River Goby *Glossogobius callidus* (Smith, 1937), and two non-native species, Mozambique Tilapia *Oreochromis mossambicus* (Peters, 1852) and Western Mosquitofish *Gambusia affinis* (Baird and Girard, 1853). The native River Goby is naturally found in estuarine and freshwater habitats (Engelbrecht and Mulder 1999; James et al. 2007). The River Goby is an invertivorous species (Wasserman 2012; Mofu et al. 2019). The non-native Mozambique Tilapia is native to eastward flowing rivers of central and southern Africa but its natural distribution does not extend to the Sundays River (Skelton 2001). The non-native Mozambique Tilapia is an omnivorous species, with clear ontogenetic shifts in diet, where juveniles feed predominantly on zooplankton and insects, while the diet of adults comprises of vegetative detritus (Zengeya et al. 2011). The non-native Western Mosquitofish is native to the lowland ponds, lakes and drainages of North America from Mexico to Alabama (Skelton 2001; Pyke 2008). It is an opportunistic omnivore feeding on algae, crustaceans, insects and amphibian larvae (Pyke 2008). Both non-native Mozambique Tilapia and Western Mosquitofish have been listed in the top 100 worst global invasive species database (IUCN 2006). Given that these three fish co-occur and are the most abundant within the Sundays River Valley irrigation ponds, this study sought to comparatively assess the potential relative ecological impacts of non-native Mozambique Tilapia and non-native Western Mosquitofish relative to the native River Goby towards native benthic prey across a seasonal temperature gradient.

Materials and methods

Ethical clearance and permits

The collection of animals and all experiments were carried out in compliance with the Eastern Cape Department of Economic Development and Environmental Affairs (DEDEA permit no. CRO 35/17CR and CRO 36/17CR) and ethical clearance was approved by the National Research Foundation – South African Institute for Aquatic Biodiversity (NRF-SAIAB reference no. 25/4/1/5_2017/03).

Functional response experimental design

River Goby, Mozambique Tilapia and Western Mosquitofish individuals were sourced using a 30 m × 2 m seine net with 12 mm mesh wings and an 8 mm mesh cod-end from

Dunbrody (33°27'53"S; 25°33'02"E) and Disco Chicks (33°27'26"S; 25°39'57"E) irrigation ponds, Eastern Cape, South Africa. Upon capture, fish were transported to NRF-SAIAB, Grahamstown in continuously aerated containers with source water. Each fish species was housed separately in a controlled temperature and light laboratory and kept under a 12:12 light:dark cycle. Temperature was maintained at either 18 ± 2 °C or 25 ± 2 °C (i.e. experimental temperature groups) for seven days prior to experimentation, with each species acclimated separately in 40 L fish tanks in a closed recirculating system. All fish were maintained on a standardized diet of larval chironomids *ad libitum*. The chironomid larvae were collected by kick sampling from the Bloukrans River (33°19'06"S; 26°34'22"E) using a kick net (1000 µm). The chironomids were then strained twice through 2.0 mm and then 1.0 mm sieves to obtain the experimental size class (total length (T_L) \pm standard deviation ((SD) 1.5 ± 0.11 mm) and then rinsed thoroughly with deionized water to remove any other food sources.

Functional response experiments were performed at 18 °C and 25 °C, reflecting respective spring and summer temperatures at the sampling locations. Following Alexander et al. (2014), all fish were size matched (T_L (mean \pm SD): River Goby = 41.50 ± 4.10 mm; Mozambique Tilapia = 41.70 ± 4.10 mm; Western Mosquitofish = 41.60 ± 4.10 mm), in order to eliminate the influence of size-related differences on prey consumption and focus on species-specific differences (Rall et al. 2012). Individuals of River Goby, Mozambique Tilapia and Western Mosquitofish were randomly selected from the holding tanks 24 hours prior to the trial and transferred to experimental arenas (opaque 20 L spherical arenas: diameter: 290 mm; depth: 400 mm) containing 5 L of continuously aerated rainwater. In individual experimental arenas, each assigned fish was held for 24 hrs prior to the experiment without food to allow for acclimatization and standardization of hunger levels. Individual fish were then presented with chironomid larvae at one of eight prey densities ($n = 2, 4, 8, 16, 32, 64, 96$ and 120 ; $n = 7$ replicates per prey density). At the end of each experimental period, predators were removed and the total number of live prey items remaining, and hence numbers consumed, enumerated. One set of experiments (i.e. one randomized fully factorial replicate per experimental temperature group) was conducted in a day, and the experiments were initiated at 09:00 am, during photoperiod, with prey consumption examined after 2 hrs. Controls consisted of larval chironomids in experimental tanks at each prey density in the absence of predators ($n = 2$ replicates per experimental group). Predators were only used once and therefore there was no re-use within or across experimental groups.

Fish abundances

The fish predator abundance data were obtained from the NRF-SAIAB's monitoring program of irrigation ponds in the Sundays River Valley, Eastern Cape, South Africa. Abundance from two irrigation ponds were used, ML Swart (33°24'33"S; 25°29'04"E), and River Bend (33°26'23"S; 25°42'25"E). The pond names represent either the property or farm owner's name, as recorded by the Lower Sundays River Water User Association. These ponds were selected on the basis that they were surveyed

in both spring and summer and that all three species were captured to give abundance estimates. During each survey, the irrigation pond water temperatures were measured using a HANNA HI98129 combo pH and electrical conductivity meter (HANNA Instruments Inc., Woonsocket, USA). Spring (18 °C) and summer (25 °C) abundance estimates were used in this study as they were in line with the experimental temperatures, and reflect seasonal temperature means.

The ponds were surveyed using a 30 m × 2 m seine net with 12 mm mesh wings and an 8 mm mesh cod-end. At least three hauls were conducted per pond and, upon completion of a single haul, all fish were kept alive in a continuously aerated container (20 L) until every seine haul was completed within a pond. Fish were then identified to species-level, enumerated and released back to the water. The abundance data were based on maximum catch field abundances using mean catch per 100 m².

Statistical analyses

Generalized linear models (GLMs) assuming a Poisson error distribution and log link were used to analyze overall prey consumption with respect to species, temperature and prey supply. Likewise, GLMs were used to compare fish abundances with respect to species, season and pond. Non-significant terms and interactions were removed step-wise to obtain minimum adequate models (Crawley 2007). Tukey's comparisons were used to undertake *post hoc* tests of significant effects in each resulting model (Hothorn et al. 2008).

To distinguish between Type II and III functional responses, logistic regression of the proportion of prey consumed as a function of initial prey density was performed (but see also Rosenbaum and Rall 2018). Selection between Type II and Type III models was further confirmed *via* comparison of Akaike's information criterion. A significantly negative first-order term indicates a Type II functional response, whereas a significantly positive first-order term followed by a significantly negative second-order term indicates a Type III response (Juliano 2001). Rogers' random predator equation was used to model functional responses as prey were not replaced as they were consumed (Rogers 1972):

$$N_e = N_0 \left(1 - \exp \left(a (N_e h - T) \right) \right) \quad (1)$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack rate, h is the handling time and T is the experiment duration (fixed at 1). To enable model fitting, the *Lambert W* function was used (needed as N_e appears on both sides of the equation; (Bolker 2008)). Differences in attack and handling parameters were assessed pairwise between fishes at each temperature using indicator variables (Juliano 2001; Pritchard et al. 2017). Bonferroni corrections were used on raw p -values to account for multiple comparisons. Multiple estimates of the handling time parameter h were generated using non-parametric bootstrapping ($n = 100$), with maximum feeding rates then calculated *via* $1/h$.

We calculated relative impact potential (RIP) of native (i.e. River Goby) and non-native (i.e. Mozambique Tilapia, Western Mosquitofish) species using the mean bootstrapped functional response maximum feeding rate (FR) and abundance (AB) for the three species at each season and pond (Dick et al. 2017):

$$\text{RIP} = \left(\frac{\text{FR non-native}}{\text{FR native}} \right) \times \left(\frac{\text{AB non-native}}{\text{AB native}} \right) \quad (2)$$

when $\text{RIP} < 1$, the predicted impact of the non-native fish is predicted to be less than the native; when $\text{RIP} = 1$, there is no difference in impact between the fish species; whereas when $\text{RIP} > 1$, the non-native has a greater impact than the native. To integrate uncertainty into the RIP score, a probability density function (pdf) was applied using the standard deviation (SD) of the FR and AB estimates and this generated 80% confidence intervals (CIs) (see Dick et al. 2017). Biplots were then generated to illustrate the RIP for both for non-native Mozambique Tilapia and Western Mosquitofish relative to the native River Goby at each season between ponds (Lavery et al. 2017). All analyses were carried out in R v. 3.4.2 (R Development Core Team 2017).

Results

Functional response

Prey survival of larval chironomids was 99% in control groups with predators absent, and thus prey mortality in the experimental groups was attributed to predation. Overall consumption was significantly different among fish species ($\chi^2 = 221.67$, $df = 2$, $p < 0.001$). Native River Goby consumed significantly fewer prey than both non-native Mozambique Tilapia ($z = 14.61$, $p < 0.001$) and non-native Western Mosquitofish ($z = 8.43$, $p < 0.001$). Mozambique Tilapia, in turn, consumed significantly more prey than Western Mosquitofish overall ($z = 6.41$, $p < 0.001$). Consumption was also significantly greater at the higher temperature, analogous with the summer season ($\chi^2 = 179.61$, $df = 1$, $p < 0.001$), and consumption increased with temperature for all species as there was no significant 'predator \times temperature' interaction ($\chi^2 = 3.54$, $df = 2$, $p = 0.171$; Figure 1). Furthermore, consumption increased significantly with increasing prey supply ($\chi^2 = 2019.88$, $df = 1$, $p < 0.001$).

At 18 °C (i.e. spring temperature), all three fish species displayed a Type II functional response (Table 1; Figure 1a). Attack rates did not differ significantly between fishes (River Goby and Mozambique Tilapia: $z = 1.03$, $p = 0.301$; River Goby and Western Mosquitofish: $z = 0.42$, $p = 0.675$; Mozambique Tilapia and Western Mosquitofish: $z = 0.51$, $p = 0.611$). However, native gobies exhibited significantly longer handling times compared to both non-native Mozambique Tilapia ($z = 9.67$, $p < 0.001$) and non-native Western Mosquitofish ($z = 4.36$, $p < 0.001$). Accordingly, maximum feeding rates were considerably higher in the non-native as compared to native fishes (Table 1). In turn, Mozambique Tilapia had significantly shorter handling

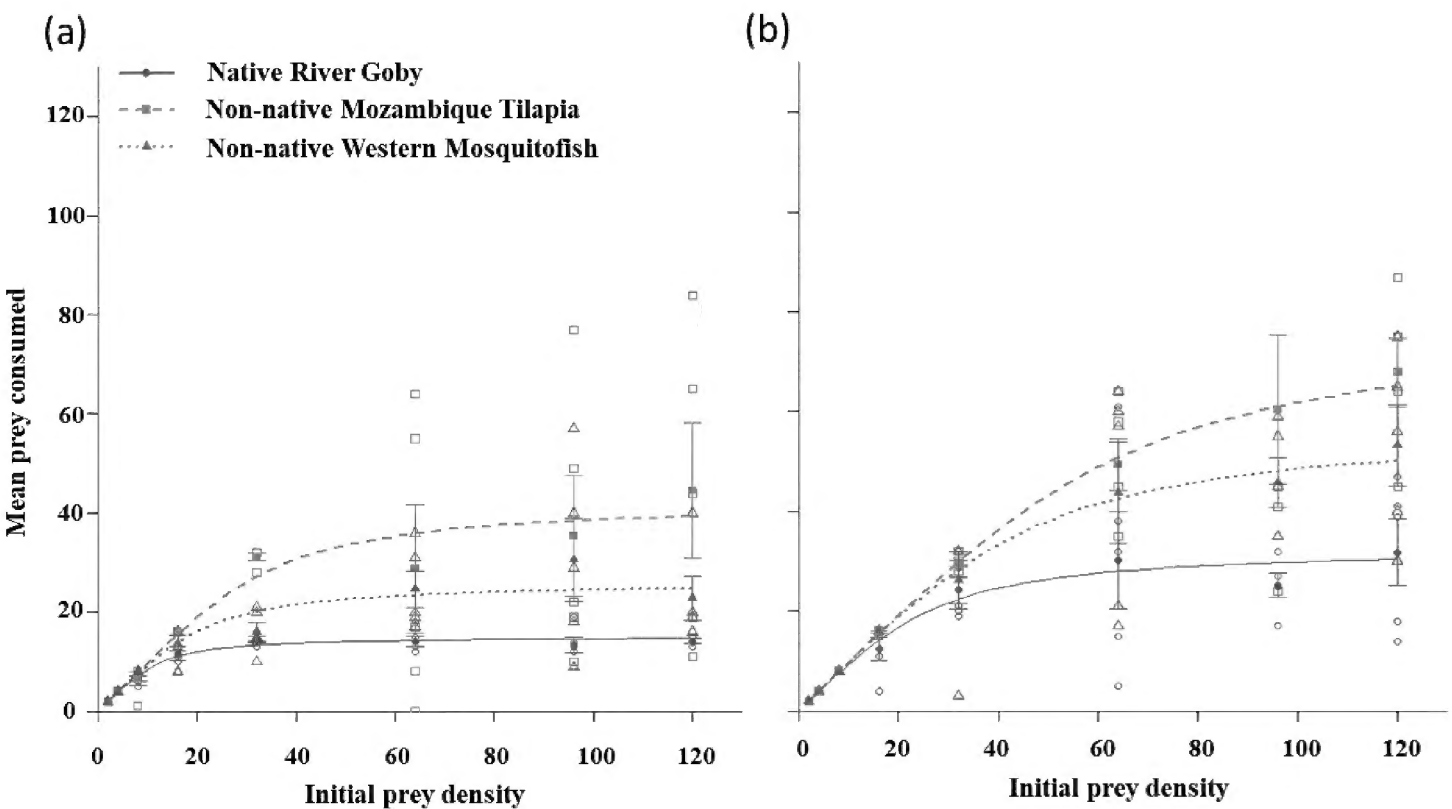


Figure 1. Functional response curves for native River Goby (blue circles, solid lines), non-native Mozambique Tilapia (red squares, dashed lines) and non-native Western Mosquitofish (green triangles, dotted lines) at 18 °C (a) and 25 °C (b). Means are \pm SE. Filled points are means and unfilled points are raw data.

times, and thus higher maximum feeding rates, than Western Mosquitofish ($z = 6.27$, $p < 0.001$) (Figure 1a).

At 25 °C (i.e. summer temperature), all three fish species also exhibited a Type II functional response (Table 1; Figure 1b). There were significant differences in attack rates between the native River Goby and the non-native Mozambique Tilapia ($z = 2.62$, $p = 0.008$). Attack rates between the native River Goby and the non-native Western Mosquitofish did not differ significantly ($z = 0.24$, $p = 0.811$). However, Mozambique Tilapia had significantly lower attack rates than Western Mosquitofish ($z = 2.88$, $p = 0.004$). Native gobies displayed significantly longer handling times than non-native Mozambique Tilapia ($z = 12.55$, $p < 0.001$) and non-native Western Mosquitofish ($z = 7.18$, $p < 0.001$), again driving substantially higher maximum feeding rates by the non-native fishes (Table 1). In turn, Mozambique Tilapia had significantly shorter handling times than Western Mosquitofish ($z = 6.92$, $p < 0.001$), and hence exhibited the highest maximum feeding rate (Figure 1b).

Table 1. Parameter estimates from first-order logistic regression of the proportion of consumed prey as a function of prey density, with rounded functional response estimates, a = attack rate; h = handling time, $1/h$ = maximum feeding rate.

Predator	Temperature	First-order term, p	a	p	h	p	$1/h$
Native River Goby	18 °C	-0.04, <0.001	4.34	<0.001	0.05	<0.001	20.00
Non-native Mozambique Tilapia	18 °C	-0.03, <0.001	5.23	<0.001	0.02	<0.001	43.48
Non-native Western Mosquitofish	18 °C	-0.03, <0.001	4.74	<0.001	0.04	<0.001	27.78
Native River Goby	25 °C	-0.03, <0.001	3.65	<0.001	0.03	<0.001	34.48
Non-native Mozambique Tilapia	25 °C	-0.01, <0.001	2.20	<0.001	0.01	<0.001	111.11
Non-native Western Mosquitofish	25 °C	-0.02, <0.001	3.80	<0.001	0.02	<0.001	58.82

Fish abundances

There was a significant 'species \times season \times pond' interaction ($\chi^2 = 92.54$, $df = 2$, $p < 0.001$; Figure 2), with seasonal responses of fish species abundance differing between the two ponds. From ML Swart in spring, native River Goby abundances were not significantly different to non-native Mozambique Tilapia ($z = 0.63$, $p = 0.988$), but were more abundant than non-native Western Mosquitofish ($z = 4.44$, $p < 0.001$). In turn, the non-native Mozambique Tilapia were also more abundant than the non-native Western Mosquitofish ($z = 4.73$, $p < 0.001$). In summer, ML Swart abundances of the native gobies did not differ significantly either to non-native Mozambique Tilapia ($z = 0.48$, $p = 0.990$) or non-native Western Mosquitofish ($z = 2.71$, $p = 0.070$). In addition, there were no significant differences between non-native Mozambique Tilapia and non-native Western Mosquitofish abundances ($z = 2.23$, $p = 0.223$). On the other hand, from River Bend in spring, native gobies were significantly more abundant than both non-native Mozambique Tilapia ($z = 4.52$, $p = 0.001$) and non-native Western Mosquitofish ($z = 6.28$, $p < 0.001$). Non-native Mozambique Tilapia abundances were significantly greater than non-native Western Mosquitofish ($z = 3.51$, $p = 0.006$). In summer, however, gobies were significantly less abundant than non-native Mozambique Tilapia ($z = 10.74$, $p < 0.001$) yet more abundant than non-native Western Mosquitofish ($z = 4.12$, $p < 0.001$). Similarly, the non-native Mozambique Tilapia were more abundant than the non-native Western Mosquitofish here ($z = 5.74$, $p < 0.001$).

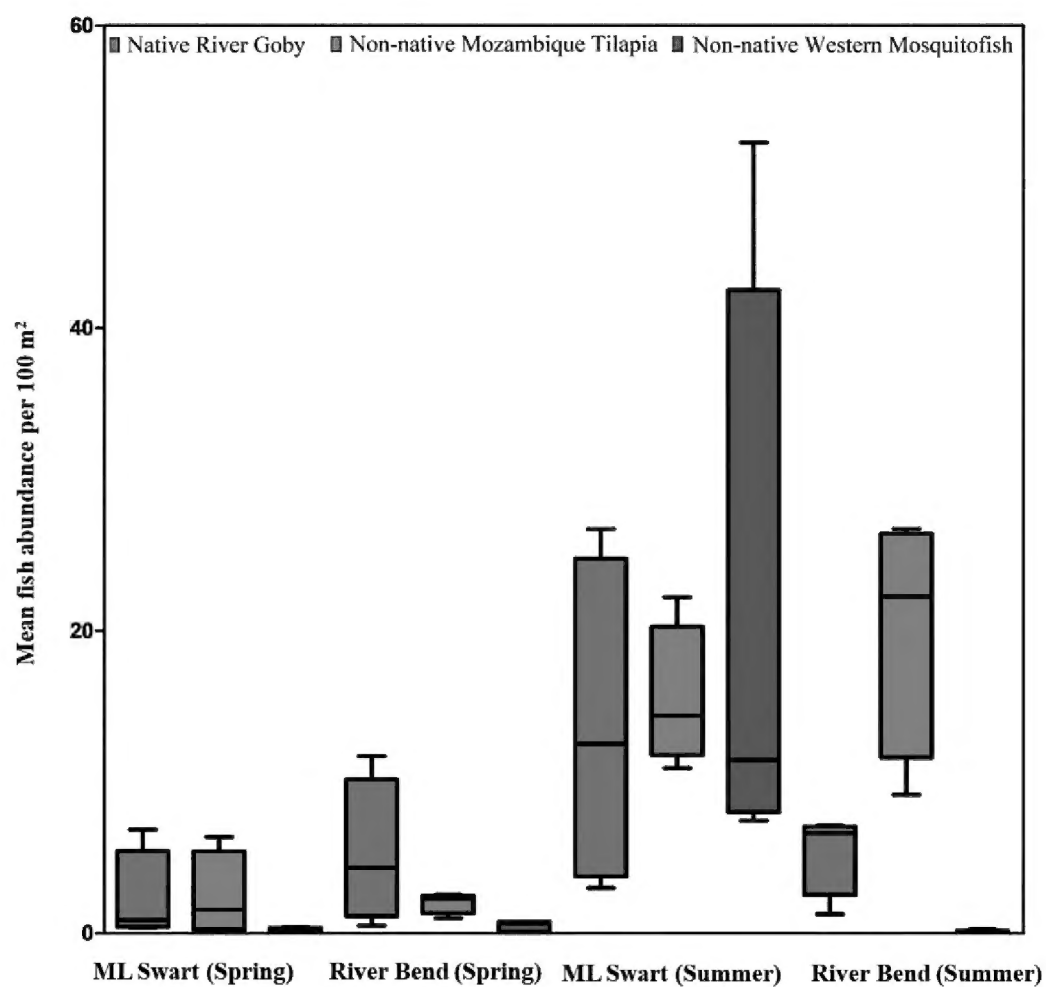


Figure 2. Abundance box plots for native River Goby (blue), non-native Mozambique Tilapia (red) and non-native Western Mosquitofish (green) from ML Swart and River Bend irrigation ponds, Eastern Cape, South Africa. Sampling occurred in spring (18 °C) and summer (25 °C).

Relative impact potential

Under both spring and summer treatments, the non-native Mozambique Tilapia consistently displayed relative impact potential scores > 1 relative to the native River Goby irrespective of focal ponds, suggesting greater impact than the native species (Table 2). In contrast, non-native Western Mosquitofish had relative impact potential scores of < 1 from ML Swart and approximately 1 from River Bend in spring, respectively suggesting lower or similar impacts to native River Goby (Table 2). In summer, non-native Western Mosquitofish had a relative impact potential score > 1 from ML Swart, but had a relative impact potential score < 1 from River Bend. This suggests less impact in River Bend and higher impact in ML Swart relative to native River Goby.

The relative impact potential biplots concur with the relative impact potential scores (Figure 3). In spring, non-native Mozambique Tilapia had the highest impact potential followed by native River Goby and lastly by non-native Western Mosquitofish in both ML Swart and River Bend (Figure 3a, b). In summer, there is inconsistency between the ponds, whereby the native River Goby has the lowest relative impact potential in ML Swart compared to the non-native Mozambique Tilapia and the non-native Western Mosquitofish (Figure 3c). The relative impact potential biplots from River Bend in summer are more reflective of the trends observed in both ponds in spring, where the non-native Mozambique tilapia had the highest impact potential followed by the native River Goby and lastly the non-native Western Mosquitofish, which had no impact owing to its absence here (Figure 3d).

Table 2. Relative Impact Potential (RIP) using mean bootstrapped maximum feeding rates for non-native Mozambique Tilapia and non-native Western Mosquitofish against native River Goby. Field abundance data are integrated from ML Swart and River Bend ponds in spring and summer. Uncertainties are reflected through 80% confidence intervals (CIs).

Species	Season	Pond	Mean FR maximum feeding ± SD	Mean field abundance ± SD	RIP	CIs	<i>P</i> _{rip} >1
Non-native Mozambique Tilapia, native River Goby	Spring	ML Swart	45.40 ± 11.31, 19.96 ± 3.53	2.41 ± 2.84, 2.25 ± 3.10	7.25	0.42 – 16.32	75.17
Non-native Mozambique Tilapia, native River Goby	Spring	River Bend	45.40 ± 11.31, 19.96 ± 3.53	2.04 ± 0.69, 5.22± 4.80	1.69	0.35 – 3.57	55.21
Non-native Western Mosquitofish, native River Goby	Spring	ML Swart	26.68 ± 2.87, 19.96 ± 3.53	0.19 ± 0.17, 2.25 ± 3.10	0.35	0.29 – 0.78	70.78
Non-native Western Mosquitofish, native River Goby	Spring	River Bend	26.68 ± 2.87, 19.96 ± 3.53	2.04 ± 0.69, 5.22 ± 4.80	1.01	0.22 – 2.11	33.40
Non-native Mozambique Tilapia, native River Goby	Summer	ML Swart	125.02 ± 54.57, 32.60 ± 4.10	15.50 ± 4.80, 13.70 ± 11.10	7.30	1.58 – 15.35	96.40
Non-native Mozambique Tilapia, native River Goby	Summer	River Bend	125.02 ± 54.57, 32.60 ± 4.10	20.10 ± 8.02, 5.41 ± 2.77	18.26	5.21 – 36.15	99.98
Non-native Western Mosquitofish, native River Goby	Summer	ML Swart	97.17 ± 148.60, 32.60 ± 4.10	20.70 ± 21.20, 13.70 ± 11.10	7.58	0.30 – 16.56	69.64
Non-native Western Mosquitofish, native River Goby	Summer	River Bend	97.17 ± 148.60, 32.60 ± 4.10	0.06 ± 0.13, 5.41 ± 2.77	0.05	0.00 – 0.09	40.20

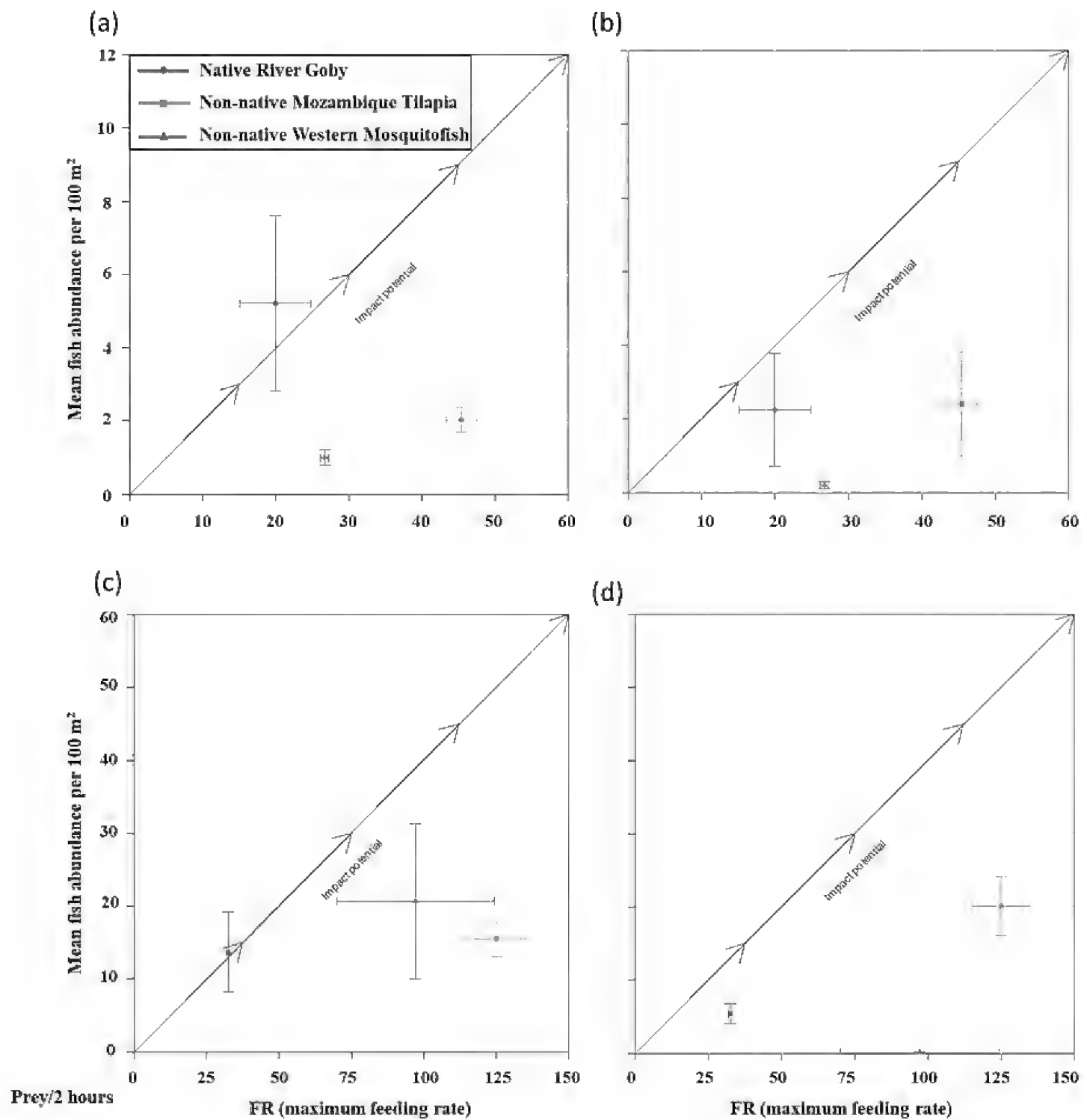


Figure 3. Relative impact potential (RIP) biplots (see also Table 2) of native River Goby (blue circles), non-native Mozambique Tilapia (red squares) and non-native Western Mosquitofish (green triangles) in spring (18 °C): (a) ML Swart (b) River Bend; and in summer (25 °C): (c) ML Swart and (d) River Bend. Ecological impact increases from bottom left to top right. Note differences in axes scaling. Values are mean \pm SD.

Discussion

Using the relative impact potential metric proposed by Dick et al. (2017), this study provides insights into how the ecological impacts of non-native species are mediated by temporal variabilities associated with seasons through the multiplying of functional responses and population abundances. Irrespective of seasonal variations, our results corroborate with studies that identified Mozambique Tilapia as a particularly impact-

ful non-native species (Canonico et al. 2005; Maddern et al. 2007), whilst Western Mosquitofish impacts were less pronounced. We first show that all three fish species display a Type II functional response across the seasonal gradient, conducive to high resource utilisation at low densities. Whilst Type II functional responses are common in comparative laboratory-based studies (e.g. Dick et al. 2013), if included experimentally, additional context-dependencies such as habitat structure may have driven a significant impact on functional response form (Vucic-Pestic et al. 2010a; Vucic-Pestic et al. 2010b; Kalinkat et al. 2013; Barrios-O'Neill et al. 2016). Moreover, greater incremental low-density prey resolution, different feeding durations and larger experimental aquaria volumes may further alter functional response forms (e.g. to Type III) (Sarnelle and Wilson 2008; Uiterwaal and DeLong 2018). Nevertheless, in the present comparative study, interspecific variation in functional responses between the species showed that both the non-native species exert higher *per capita* impacts than the native species on native prey and that predatory impacts are more profound during the summer season. These findings concur with a considerable number of studies comparing impact between invasive and native species (Alexander et al. 2014; Dick et al. 2014; Cuthbert et al. 2019).

Temperature differences had a significant effect on the functional response parameters, wherein attack rates were high in spring (i.e. 18 °C) and were reduced in summer (i.e. 25 °C). This result concurs with Grigaltchik et al. (2012), where an increase in temperature resulted in reduced attack rates, but contrasts with other studies (e.g. Wasserman et al. 2016) wherein attack rates exhibit a non-monotonic temperature response. Furthermore, we showed that during the summer season, handling times were reduced and hence these species exhibited higher maximum feeding rates. The findings from Englund et al. (2011) corroborate with ours, and this effect is mostly related to predators' metabolic rate changes. For instance, for a predator's metabolic activity to reach its maximum efficiency (i.e. high *per capita* effects), temperatures need to be optimal; yet if temperatures are too high this will result in reduced metabolic rates through catabolism (Clarke and Johnson 1999).

Secondly, we show that there was significant variation in fish abundances among species according to season, and also between ponds. Such variation in fish abundances seems to be a common theme, especially in fish communities that co-occur in environments and this is driven by spatial and temporal variation in life-history traits (Amezcuza and Amezcua-Linares 2014). All three fish species were generally less abundant in spring and more abundant in summer. Mozambique Tilapia were the most abundant species overall, followed by River Goby and, lastly, Western Mosquitofish. By combining the fish maximum feeding rates and abundances (as per Dick et al. 2017) to give the relative impact potential score, we showed that the non-native Mozambique Tilapia consistently had the highest impact across seasons whereas, in the majority of cases, impacts of non-native Western Mosquitofish were less apparent relative to the native River Goby given currently low abundances.

Changes in relative impact potential scores with seasonal temperature fluctuations and fish abundances from different localities demonstrate how such context-dependencies can have a critical effect on the relative field impact capacities of introduced

species through time (Dick et al. 2017). The effects of temperature regime shifts on interaction strengths are profound across habitat types and trophic groups (Englund et al. 2011; Rall et al. 2012), and increasing temperatures may exacerbate invader ecological impacts as species approach thermal optima (Iacarella et al. 2015). This is supported by the heightened functional responses observed for the non-native Mozambique Tilapia and non-native Western Mosquitofish as experimental temperature was increased to near their thermal preferendum ($\sim 28^{\circ}\text{C}$; Jobling 1981). Therefore, the explicit inclusion of temperature change will be critical in future studies which seek to predict invader impacts across regime shifts associated with climatic warming and seasonal variability. Since the relative impact potential metric was 100% predictive of ecological impact across taxonomic and trophic groups (Dick et al. 2017), the current results, whereby relative impact potential is high for the non-native Mozambique Tilapia, gives confidence that this species can be forecast to cause major ecological impacts.

The present study further demonstrates the usefulness of numerical response proxies such as abundances in rapid assessments of potential impacts of introduced species. Indeed, in many cases, impact predictions are inherently limited if based on *per capita* impacts alone, given the importance of abundances in discernments of overall offtake rates by consumer populations (Dick et al. 2017). Importantly, our results suggest that ecological impacts of non-native species are likely to change across seasonal gradients associated with both changing functional responses and abundances, with summer impacts generally more profound than those in spring. We thus propose that further studies should incorporate such seasonal variability. Our study demonstrates that species-specific shifts in abundances may alter interaction strengths within ecosystems towards native populations. Therefore, quantitative assessments of species abundances can ultimately bridge the gap in decision-making and can be used to forecast future invader impacts under different climatic conditions when combined with *per capita* effects. Nevertheless, our study additionally demonstrates that individual systems (e.g. ponds) can differ substantially in predator community composition over time, and this system-specific population variability should be also considered in future studies.

Overall, this study provides further evidence of the strength of the relative impact potential metric in predicting ecological impacts of species and provides an extension to the framework by integrating an environmental gradient, which reflects seasonal temperature fluctuations. The identification of temporal shifts in impact across seasons and habitats in our study presents novel insights into invader impact. In many ecosystems, data on species abundances are still lacking, but since the relative impact potential metric enables impact predictions for species without invasion histories, we recommend more surveys to estimate abundance of potential invaders and/or for practitioners to incorporate other proxies (such as fecundity) into the metric (see Dickey et al. 2018). Crucially, the ability of both Mozambique Tilapia and Western Mosquitofish to thrive in novel habitats highlights their ecological plasticity, and with an increase in environmental temperatures, their impacts may be intensified through changes to functional responses and fish abundances. The relative impact potential metric thus allows for rapid assessment of current and future invasive species under shifting environmental contexts and can identify priority species for management.

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